Meteorological conditions and site characteristics driving edible mushroom production in *Pinus pinaster* forests of central Spain

Authors:

Zelalem Mengiste Taye[1]*****, Fernando Martínez-Peña[2,3], José Antonio Bonet[1,4], Juan Martínez de Aragón[4], Sergio de-Miguel[1,]**

Affiliations:

[1] Departament de Producció Vegetal i Ciència Forestal, Universitat de Lleida-Agrotecnio Center (UdL-Agrotecnio), Av. Rovira Roure, 191, E-25198 Lleida, Spain

[2] Center for Agro-Food Research and Technology of Aragon (CITA), 50059-Zaragoza, Spain

[3] Cesefor foundation. 42005-Soria, Spain

[4] Àrea de Productes Forestals no Fustaners, Centre Tecnològic Forestal de Catalunya (CTFC-CEMFOR), Ctra. De St. Llorenç de Morunys, km. 2. E-25280 Solsona, Spain

***** Current address: Bahir Dar Universtiy, College of Science. Department of Biology. Bahir Dar, Ethiopia

** Corresponding author

E-mail addresses: selamlehulu1@yahoo.com (Z.M. Taye), fmartinezpe@aragon.es (F. Martínez-Peña), jantonio.bonet@pvcf.udl.cat (J.A. Bonet), mtzda@ctfc.cat (J. Martínez de Aragón), sergio.demiguel@pvcf.udl.cat (S. de-Miguel)

Abstract

Integrating fungal-based ecosystem services into forest management planning and policy-making requires quantitative knowledge on the yields of fungal sporocarps and their environmental drivers. The aim of this study was to predict edible mushroom yield in *Pinus pinaster* forests of Central Spain, based on a 17-year data series. Two-stage mixed-effects models were used to examine the effect of predictors on mushroom occurrence and yield separately with the aim of providing further insight into the ecological system. Changes in seasonal precipitation represented the main weather-related driver affecting sporocarp emergence and production, since they were both positively influenced by late summer and early autumn precipitation. Soil acidity positively influenced *Lactarius* yield. Stand age and sandy soils showed a negative influence on mushroom production. The diversity of drivers became more apparent at the fungal species level. The models can be used for predicting the production of edible fungi under different meteorological and site conditions.

Key words: *Lactarius deliciosus*, fungi, non-wood forest product, mixed-effects, modeling, occurrence, yield, environmental drivers, pine

1. Introduction

Wild edible fungi are among the most important non-wood forest products (NWFPs) due to their commercial and recreational importance as a food source (Boa, 2004). Therefore, they represent a key element of provisioning and cultural fungal-based ecosystem services such as wild food, leisure, tourism and marketed goods (Martínez de Aragón *et al*., 2011; Schulp *et al*., 2014). Indeed, the market demand for many ectomycorrhizal fungi has increased to the extent that the value of forest fungi may equal or even surpass the value of timber (Alexander *et al*., 2002; Palahí *et al*., 2009). Central Spain, where mushroom harvesting has become a major activity in *Pinus pinaster* forests (Fernández-Toirán, 2006), is not an exception, and the revenue from mushroom collection is approaching the return expected from timber, which has been the most important forest product during the last decades (Ágreda *et al*., 2013). Some of the fungi found in *P. pinaster* forests, such as *Lactarius* group *deliciosus*, are highly appreciated locally and internationally, and their trade has become an important complementary economic activity in many regions (Voces *et al*., 2011; Cai *et al*., 2011; Martínez de Aragón *et al*., 2011).

The increasing socioeconomic importance of wild edible mushrooms coupled with other factors like the decrease in the profitability of wood production is making forest and land managers increasingly consider inventorying and predicting fungal yields, to integrate edible mushroom production into forest management planning (Pilz and Molina, 2002; Mogas *et al*., 2006; Aldea *et al*., 2014). The integration of mushroom production into forest management planning requires quantitative knowledge on, and prediction of, edible mushroom yields and its environmental drivers. Several factors affecting mushroom yield and dynamics have been indicated in the literature. These factors are classified into three main groups; which are stand structure (e.g. tree species, stand density, stand age), weather variability (e.g. precipitation, temperature) and local site characteristics (e.g. altitude, slope, aspect) (Martínez-Peña *et al*., 2012a). The large number of potential variables related to mushroom productivity, and their interdependence, makes it difficult to estimate mushroom yields. According to previous research, beyond stand structure or site characteristics, the variables that affect mushroom yield the most are related to meteorological conditions (Martínez-Peña *et al*., 2012b; Bonet *et al*., 2012; Hernández-Rodríguez *et al*., 2015).

Modeling techniques are valuable tools that allow identifying factors most relevant for predicting mushroom yield. Empirical models based on long historical data series of annual measurements in many locations can be used to model mushroom yields as a function of different types of predictors. In general, there are very few models in the literature aiming at predicting the yield of non-wood forest products to be used in forest planning (Bravo *et al*., 2011). Although these kinds of studies are rather recent, several mushroom yield models have been published so far (Bonet *et al*., 2008, 2010, 2012; Martínez-Peña *et al*., 2012b; de-Miguel *et al*., 2014; Ágreda et al. 2015; Hernández-Rodríguez *et al*., 2015). Mushroom yield modeling requires large quantities of data over several years in order to provide reliable estimates, especially if the models are intended to account for the effect of meteorological conditions. The difficulty in obtaining such long historical datasets for modeling the effect of weather variables is the reason behind the rather limited number of such mushroom yield models.

The aim of this study was to develop models for estimating the occurrence and production (i.e., fresh weight) of edible mushrooms in *P. pinaster* forests of Central Spain in relation to the provision of fungal-based provisioning ecosystem services, by accounting for the effect of stand, site and meteorological conditions based on data gathered during seventeen consecutive years (1997-2013).

2. Materials and Methods

2.1. Study area

The study area was located in the so-called “Pinares Llanos de Almazán” area, Soria province, Castilla y León region, Central Spain (Figure 1). Altitude ranges from 1,000 to 1,200 m.a.s.l. and soils are arenosols and regosols developed over tertiary and quaternary sands. The annual mean temperature is 10.6 °C, the daily mean maximum temperature is 16.7 °C, and the annual absolute maximum temperature is 38 °C. The daily mean minimum temperature is 4.5 °C, and the annual mean minimum temperature is -9.7 ºC with an absolute minimum temperature of -15 °C. The coldest and warmest months are January (mean daily minimum temperature = 1.8 °C) and July (mean daily maximum temperature = 28.1 °C), respectively. Average annual rainfall is 523.8 mm with a summer drought period typically occurring from mid-July through August. The monthly mean rainfall is 44.3 mm with a maximum event of 234.3 mm in October. Autumn season covers from late September to late December. There are 2,142 sun hours a year, with annual mean atmospheric pressure range from 868.4 hPa to 911.0 hPa.

The study area is located in natural *Pinus pinaster* stands around the Duero river basin, which are characterized by a considerable human impact as a result of their historical intensive use for resin tapping and, more recently, for timber production. The understory is formed by different shrubs (*Cistus laurifolus* L., *Juniperus communis*, *Erica arborea*, *Calluna vulgaris*) and *Quercus pyrenaica* resprouts. The rotation length of such stands is 80 years using a two-stage strip clearcutting method in which some parent trees are kept within the stand after the first cut for ten additional years to provide seeds for natural regeneration. When natural regeneration is not achieved, soil harrowing coupled with sowing or planting is carried out.

2.2. Sampling

Fifteen sample plots, established as described in Fernández-Toirán *et al*. (2006) and Ágreda *et al*. (2013), were used representing different stand age classes. Each plot covered an area of 150 m^2, with a rectangular shape (5×30 m). Plots were fenced to prevent harvesting and trampling. Plots were located at least 500 m from stands of another age class in the forest management plan, and areas with other tree species present were avoided. Since the study area is very flat, there was little difference in slope and aspect between plots.

Soil texture, organic matter and pH were determined for each plot at the beginning of the study. Weather data were obtained from the nearest meteorological station to the study area (Lubia-CEDER, Almazán, Soria), located 15 to 30 km far from the sampled stands. Since the study plots are located in a plateau sharing the same climatic conditions, the weather data from this meteorological station can be considered as representative of the weather conditions of the mushroom plots. In 2012, the age of every tree in each plot was determined by tree ring analysis. For every plot, mean stand age and age of the oldest tree were then assigned for the whole study period, 1997 to 2013.

Mushroom inventory was performed every week from September to December (week 35–50) (i.e., the period which corresponds with most of the sporocarp emergence; maximum production occurring in October and November) for 17 years (i.e., from 1997 to 2013). All sporocarps were collected, and the edible fungal species were determined based on morphological features.

2.3. Data

A total of 41 edible mushroom species were identified, of which non-marketed and marketed were represented by 33 and 8 species, respectively (Table 1). *Lactarius* group *deliciosus*, which includes *L. deliciosus*, *L. sanguifluus* and *L. semisanguifluus*, represented 76% of all marketed mushroom yield in fresh weight, whereas marketed mushrooms represented 45% of the yield of all edible mushrooms. The data were characterized by high inter-annual variability in mushroom occurrence and yield associated with differences in weather and site conditions (Figs. 2 and 3). A summary of the modeling data and their correlations are shown in Table 2 and Figure 4.

2.4. Modeling

The aim was to model mushroom yield for the following groups of fungi separately: edible, marketed and *Lactarius* group *delicious*. Thus, the response variables were designed by pooling the occurrence and yield data of all fungal species according to the three levels of grouping. The fresh weight was selected as the response variable since this is the way wild edible mushrooms are usually commercialized. The predictors tested in model fitting represented meteorological conditions (i.e., monthly total rainfall and mean temperature), soil properties (i.e., organic matter content, texture and pH) and stand characteristics (i.e., stand age). Different combinations and transformations of predictors were tested. Weather variables were aggregated in different ways, e.g., the accumulated precipitation during August and/or September (late summer) or during September and/or October (early autumn), to further test their combined effect on the response variables in addition to testing the influence of the disaggregated monthly rainfall and temperature. The different combinations of weather-related variables also aimed at testing hypothetical delayed responses of mushroom yield to the combined effect of different predictors (e.g., previous research has reported a delay of several weeks in the combined effect between rainfall events and favorable temperatures) (Martínez de Aragón *et al.*, 2007; Martínez-Peña *et* *al*., 2012b). Several transformations of the predictor variables (e.g., using square root or natural logarithm) were also computed to test different possible relationships between them and the response variables. Furthermore, quadratic terms and transformations were also tested to further examine hypothetical non-linear relationships (e.g., increasing-decreasing trends) between predictors and response variables.

The rather small size of sample plots coupled with the spatio-temporal stochasticity of sporocarp emergence is likely to result in zero-inflated mushroom yield data. To avoid problems arising from the zero-inflation in our data (i.e., 13.73% of edible, 39.22% of marketed and 53.73% of *Lactarius* group *deliciosus* records were "zero" yield) we used a two-stage modeling approach to build so-called hurdle models within a generalized linear mixed-effects modeling framework (GLMM). The first part of the hurdle models aimed at predicting the probability of occurrence of mushroom production based on binomially distributed data (i.e., absence or presence) using logistic regression (Eq. 1) along with a logit link function (Eq. 2). The second part of the hurdle models aimed at predicting mushroom yield conditional on the probability of mushroom occurrence by means of Gamma regression (Eq. 3) along with a log link function (Eq. 4). Finally, the expected mushroom yield was obtained by multiplying the estimates provided by Eq. 1 and Eq. 2 (Eq. 5). In addition to dealing with zero inflation, hurdle models have the advantage of accounting for two separate states (Hamilton and Brickell, 1983) which, as compared with single-model functions, can provide further insight into mushroom dynamics by analyzing those factors driving mushroom occurrence and abundance separately (de-Miguel *et al*. 2014).

Since the modeling data were characterized by repeated measurements of mushroom yield (i.e., repeated observations for the same plot in consecutive years) (Fig. 3), year random effects were included in the models, allowing the intercept to vary randomly between years. Plot random effects were also considered in the analysis, but their variance was practically zero and, in consequence, they were removed from the final models. The analyses were carried out using "glmer" function in "lme4" package in R software (Bates *et al.*, 2014; R Core Team, 2014).

$$p(y_{ij} = 1|x) = \pi(x) = \frac{1}{1+e^{-[(\alpha_0 + a_{0j}) + \alpha \mathbf{X}_{ij1}]}} \qquad \text{Equation 1}$$

$$g(x) = \log\left[\frac{\pi(x)}{1-\pi(x)}\right] = (\alpha_0 + a_{0j}) + \alpha \mathbf{X}_{ij1} \qquad \text{Equation 2}$$

$$yield_{cij} = e^{\beta_0 + b_{0j}} \mathbf{X}_{ij2}^{\beta} \qquad \text{Equation 3}$$

$$g(x) = \log\left(e^{\beta_0 + b_{0j}} \mathbf{x}_{ij2}^{\beta}\right) = \beta_0 + b_{0j} + \beta \log(\mathbf{X}_{ij2}) \qquad \text{Equation 4}$$

$$yield_{ij} = p(y_{ij} = 1|x) \cdot yield_{cij} \qquad \text{Equation 5}$$

where $p(y_{ij} = 1|x)$ is probability of occurrence of edible, marketed or *Lactarius* group *deliciosus* mushrooms in plot *i* and year *j*, $yield_{cij}$ is edible, marketed or *Lactarius* group *deliciosus* mushroom yield conditional on mushroom occurrence in plot *i* and year *j* (kg ha^{-1} yr^{-1}) , $yield_{ij}$ is the predicted edible, marketed or *Lactarius* group *deliciosus* mushroom yield in plot *i* and year *j* (kg ha^{-1} yr^{-1}), α and β denote fixed-effects, a_{0j} and b_{0j} denote year random effects, and $\mathbf{X}_{ij1}$ and $\mathbf{X}_{ij2}$ denote vectors of predictor variables in plot *i* and year *j*.

2.5. Model selection and evaluation

Several criteria were considered in model selection and evaluation. On one hand, model selection considered whether alternative models behaved logically. That is, whether they represented biologically or ecologically consistent relationships between predictors and the response variables according to current scientific and expert knowledge. Only those models whose coefficients were statistically significant (p<0.05) were further considered in the analysis. Since overfitting may lead to poor predictive performance, we aimed at obtaining parsimonious models along with acceptable fitting statistics (i.e., low residual standard errors, and agreement with the assumptions behind different model types). Model selection was based on an iterative process mainly driven by forward selection of appropriate predictors. Furthermore, since it has been proved to be asymptotically equivalent to leave-one-cluster-out cross validation in mixed-effects models (Fang, 2011), the Akaike Information Criterion (AIC) drove model selection to prevent overfitting by accounting for the trade-offs between model parsimony and fitting statistics. Furthermore, uncertainty was assessed using resampling techniques, namely bootstrapping based on 2,000 bootstrap samples with replacement, to ensure the stabilization of the estimates, and by computing prediction and confidence intervals accounting for the residual variance, the uncertainty in the fixed coefficients, and the uncertainty in the variance parameters of the year random effects. In addition, receiver operating characteristic (ROC) curves and the corresponding area under the ROC curve (AUC) along with their bootstrapped confidence intervals were computed for the logistic models for the probability of mushroom occurrence. Similarly, uncertainty was further assessed by computing bootstrapped confidence intervals also for the year random effects of the hurdle models, as well as for the error term of the conditional yield models.

3. Results

3.1. Models for the probability of mushroom occurrence

The models selected for predicting the probability of occurrence of edible, marketed and *Lactarius* group *deliciosus* mushrooms according to the model selection and evaluation criteria are presented in Table 3 (i.e., denoted as Equation 1) along with the information about the uncertainty of the estimates. Similarly, the corresponding standard deviation of the year random effects are presented in Table 4 along with their bootstrapped confidence intervals.

The logistic regression analyses showed that the accumulated precipitation during late summer and early autumn (i.e., the sum of the total rainfall of August, September and October) was the most significant meteorological predictor of the probability of occurrence of edible, marketed and *Lactarius* group *deliciosus* mushrooms. The models indicate that higher precipitation increases the probability of occurrence of the three categories of mushrooms. In the logistic models for edible and marketed mushrooms, no other variables had a significant effect on the probability of occurrence of sporocarps. On the contrary, soil pH was also a significant predictor of the probability of occurrence of *L.* group *deliciosus* sporocarps, indicating higher probability of *Lactarius* with decreasing soil pH, that is, with increasing soil acidity.

The bootstrapped ROC curve confidence intervals and their corresponding AUC values revealed reasonably good predictive performance of all logistic regression models. The ranges (in percentage) of AUC associated with the models for the probability of edible, marketed and *Lactarius* group *deliciosus* mushrooms were 91-97, 82-91 and 81-90%, respectively, where the 100% level represents perfect predictive performance. The probability models also yielded biologically and ecologically consistent estimates among the three levels of grouping of edible sporocarps. Thus, for a given level of accumulated late summer and early-autumn precipitation (i.e., the other influential predictors remaining constant), the predicted probability of occurrence of any edible mushroom was always higher than the probability of occurrence of marketed mushrooms. Similarly, the predicted probability of occurrence of marketed mushrooms was always higher than the probability of occurrence of *Lactarius* group *deliciosus* mushrooms. The uncertainty around the expected probability of occurrence of edible mushrooms decreased considerably with increasing precipitation (Figures 5 and 6).

The standard deviation of year random effects tended to decrease as we narrowed down from the maximum level of aggregation of fungi (i.e., edible mushrooms) to the marketed and *Lactarius* group *deliciosus* levels (Table 4), which suggests that there was higher between-year variation in those grouping levels with higher number of mushroom species (Fig. 7). When alternative models were tested without allowing for such random-effects, the statistical significance of the meteorological variables increased, which suggests that year random effects contributed to explaining part of the between-year variation arising from annual changes in the meteorological conditions. Similar trends were observed when fitting equations for the second part of the hurdle models to obtain estimates of mushroom yield conditional on the probability of mushroom occurrence (Fig. 7). Despite the reasonably good performance of the models, there was considerable latent variability in the estimates of the probability of occurrence of sporocarps that could not be explained by the available data.

3.2. Models for mushroom yield conditional on the probability of mushroom occurrence

The models selected for predicting the yield (kg ha^{-1} yr^{-1}) of edible, marketed and *Lactarius* group *deliciosus* mushrooms conditional on their probability of occurrence according to the model selection and evaluation criteria are presented in Table 3 (i.e., denoted as Equation 3) along with the information about the uncertainty of the estimates. Similarly, the corresponding standard deviation of the residuals and year random effects are presented in Table 4 along with their bootstrapped confidence intervals.

The only significant predictor of edible mushroom yield conditional on mushroom occurrence was the total precipitation in September. The model predicts that increasing precipitation increases edible mushroom yield. On the other hand, both the precipitation in September and stand age (i.e., defined as the age of the oldest tree in a stand) showed a statistically significant effect on marketed mushroom yield conditional on mushroom occurrence. The precipitation in September had a positive influence on the abundance of marketed sporocarps, whereas marketed mushroom yield decreased with increasing stand age. The number of significant predictors for *L.* group *deliciosus* yield conditional on the probability of mushroom occurrence was higher. Thus, the model predicts that *Lactarius* yield increases with increasing precipitation in September and October, and on soils with loamy sand or sandy loam textures as compared with sandy soils. In contrast, *Lactarius* yield is expected to decrease with increasing stand age. The percentage of the total variance explained by the between-year variation described by the year random effects in the conditional yield models for edible, marketed and *Lactarius* group *deliciosus* mushrooms was 43%, 15% and 25%, respectively. Similar to the logistic regression models, this suggests that higher between-year variation in mushroom yield was found in the category involving a higher number of mushroom species (Fig. 7).

The expected relationship between observed and predicted values followed rather well the 1:1 equality line that denotes perfect fit (Fig. 8). Therefore, most of the disagreement between predictions and observations arose from the scatter due to the considerable unexplained variation of mushroom yield. The model for edible mushroom yield conditional on the probability of mushroom occurrence resulted in almost perfect overlap between the relationship of observed *versus* predicted values and the perfect equality line, which suggests absence of any systematic estimation bias. In the case of marketed mushrooms, model predictions also practically overlapped the perfect equality line throughout the range of observed values, with a very slight deviation. The agreement between observations and predictions as compared to the perfect equality line was also acceptable for *L.* group *deliciosus* along the range of values where most observations fall, although the model tended to slightly overestimate very low yield, and underestimate maximum yields.

3.3. Hurdle model predictions

The predictions from hurdle models reflected the combined effects of the two separate states leading to mushroom yield estimates, namely by multiplying the estimates of the probability of mushroom occurrence by the estimates of mushroom yield conditional on mushroom occurrence (Fig. 9). Thus, the effect of meteorological conditions on mushroom yield was modulated by soil properties (i.e., soil pH and texture) and stand characteristics (i.e., stand age), and *vice versa*. Mushroom yield increased with increasing accumulated precipitation during late-summer and early-autumn, as well as with increasing soil acidity and with decreasing proportion of sand in the soil. On the other hand, mushroom yield tended to decrease with increasing stand age. The hurdle models resulted in biologically and ecologically consistent estimates among the three levels of grouping of edible sporocarps. Thus, for a given level of accumulated late-summer and early-autumn precipitation (i.e., the other influential predictors remaining constant), the predicted yield of all edible mushrooms was higher than the yield estimates of marketed mushrooms. Similarly, the predicted yield of *Lactarius* group *deliciosus* mushrooms was lower than the expected marketed mushroom yield. The uncertainty in the prediction of mushroom yield tended to increase proportionally with increasing mushroom yield. In consequence, the uncertainty in the prediction was higher for edible mushroom yield as compared with marketed and *Lactarius* species groups. This was also probably due to the fact that precipitation was the only significant predictor in both stages of the hurdle model for edible mushroom yield, whereas the statistical significance of additional predictors in the marketed and *Lactarius* group *deliciosus* mushroom yield models contributed to reducing the uncertainty around the expected yield.

4. Discussion

Our results show the strong influence of the meteorological conditions on the appearance of fungal fruit bodies and mushroom yield. It was seen that stand and soil characteristics become significant predictors as we narrow down from a broad category like edible fungi to the species level of *Lactarius* group *deliciosus*. This revealed the distinct autecology and requirements of different fungal genera and species for sporocarp fructification and mushroom productivity. The higher between-year random variation with increasing species richness found in the probability of mushroom occurrence and yield models may also reflect the underlying multiplicity of ecological strategies and niches in a broader category (e.g., edible fungi, with 41 species) as compared for instance to the *Lactarius* group *deliciosus* (with only three species that, in addition, share the same genus). In any case, this does not detract from the interest of providing quantitative knowledge and models for the production of target mushroom groups associated with important provisioning ecosystem services associated with edible and marketed fungi (Martínez de Aragón *et al*., 2011; Schulp *et al*., 2014). The accumulated precipitation from late summer until mid-autumn is a driving factor for the occurrence of edible, marketed and *L.* group *deliciosus* mushrooms in *P. pinaster* forests in Central Spain, whereas mushroom yield was found to be driven mainly by the precipitation in September and, in the particular case of *Lactarius* species, by the rainfall from September through October. The models reflect the importance of not only the amount of rainfall, but also its distribution, on mushroom production.

Previous research has also indicated that mushroom production is strongly related to weather conditions, especially rainfall during the autumn season (Bonet *et al*., 2004; Martínez de Aragón *et al.*, 2007; Martínez-Peña *et al*., 2012b; Bonet *et al.*, 2012; Ágreda et al. 2015).

Although previous research has reported that temperature may be another important driver for mushroom yield (Martínez-Peña *et al*., 2012b; Hernández-Rodríguez *et al.*, 2015), no significant effect of temperature was found in this study. One possible reason for this is that temperature may become more limiting in colder areas, where frosts may inhibit the emergence of fruiting bodies (Hernández-Rodríguez *et al.*, 2015; Martínez-Peña *et al.*, 2012b). Furthermore, as already explained above, the year random effects considered in model fitting may also account for some of the between-year variation in meteorological conditions.

Our results indicated that, even though mushroom production occurred across all stand ages, maximum yield of marketed and *Lactarius* group *deliciosus* mushrooms occurred in younger stands. This is in line with previous research on the effect of stand age on the yield of *L. deliciosus* and other ectomycorrhizal fungi (Smith *et al.*, 2002; Fernández-Toirán *et al*., 2006; Bonet *et al*., 2010; Ágreda *et al*., 2013), although some authors have also reported high yields at different stand ages (Zamora-Martínez and Nieto de Pascual, 1995; Bonet *et al.*, 2004; Martínez-Peña *et al*., 2012a). Since marketed and *L*. group *delicious* species are all ectomycorrhizal fungi, they may get more carbohydrates from the more photosynthetically active trees in young stands. So, marketed mushroom production may be enhanced by maintaining young stands or by regulating stand density through forest management and thinning operations (Bonet *et al*., 2012).

We found a significant effect of pH and soil texture on *L*. group *deliciosus* yield indicating preference for rather acidic soils with loamy-sand to sandy-loam textures. Martínez-Peña *et al*. (2012b) reported strong correlations between soil variables such as pH, texture or water retention capacity and mushroom yield in *Pinus sylvestris* forests. They found negative correlation of sand content with *Lactarius* yield, whereas silt and clay content in the soil were positively correlated with the production of saffron milk caps. This could be due to the fact that sandy soils have lower water holding capacity than loamy-sand and sandy-loam soil textures. Furthermore, the fact that our models predict higher *Lactarius* group *deliciosus* yield on sandy-loam than on loamy-sand textures is also consistent with this hypothesis since sandy loam soils tend to have higher water retention capacity than loamy sands (Moore *et al.*, 2001). Since the area is characterized by a pronounced summer drought, water-holding capacity of the soil could be critical to maintain certain moisture conditions within the soil. Our results also showed a negative relationship between pH and occurrence of *L.* group *deliciosus*, which is in line with previous research suggesting better performance of *Lactarius* in the acidic range. Barros *et al*. (2006) showed that the growth of *L. deliciosus* mycelium is significantly better in the slightly acidic soil (pH=5), but the effect of pH was dependent on the medium they used. González-Ochoa *et al*. (2003) observed higher percentage of colonization for *Lactarius* genus on acidic soils (pH=4.5-5.5) in a study conducted in two commercial nurseries. On the other hand, the genus *Lactarius* has been reported as being only slightly affected by variations in pH (Espigol, 1999), although the response may be different for different *Lactarius* species.

However, there was a considerable latent variability associated with the models that could not be explained from the available data. This is common in studies dealing with fungal dynamics since there is uncertainty arising from a number of reasons: (i) the cryptic nature of fungi, (ii) the poor knowledge of belowground fungal dynamics, and their effect on aboveground dynamics, (iii) the intrinsic randomness of fungal species occurrence, (iv) the poor knowledge about fungal species interactions, (v) the unavailability of more detailed stand, site and microclimatic data at the plot level, and (vi) the rather homogeneous conditions of the study area, along with many other sources of uncontrolled variability.

Considering the increasing interest in the multifunctionality of forest ecosystems and non-wood forest products, this study throws light on the factors that affect edible mushroom production. We provide models for predicting the probability of occurrence and the yield of edible, marketed and *L.* group *deliciosus* mushrooms in *P. pinaster* forests in Central Spain. The two-stage modeling approach allowed us to assess the effect of the weather, soil and stand variables on mushroom dynamics by describing, separately, the drivers of sporocarp emergence and mushroom abundance. This has provided further insight into the ecological system. Furthermore, these models can help silviculturalists and forest policy makers interested in the provision of fungal-based ecosystem services in decision making, not only about suitable rotation lengths, but also in the identification of areas of greater potential for mushroom yield according to site conditions. However, further research is needed to better understand the combined effect of different drivers on mushroom yield by for instance broadening the spatial scale and by incorporating additional potential drivers into the analysis. Further research based on the models provided in this study could also be devoted to further assessing the influence of alternative climate change scenarios on edible mushroom occurrence, distribution and yield.

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References

Ágreda, T., Águeda, B., Olano, J.M., Vicente-Serrano, S.M., Fernández-Toirán, L.M., 2015. Increased evapotranspiration demand in a Mediterranean climate might cause a decline in fungal yields under global warming. Global Change Biology, doi: 10.1111/gcb.12960.

Ágreda, T., Cisneros, O., Águeda, B., Fernández-Toirán, L.M., 2013. Age class influence on the yield of edible fungi in a managed Mediterranean forest. Mycorrhiza. 24:143-152.

Aldea, J., Martínez-Peña, F., Romero, C., Díaz-Balteiro, L., 2014. Participatory goal programming in forest management: an application integrating several ecosystem services. Forests. 5: 3352-3371.

Alexander, S.J., Pilz, D., Weber, N.S., Brown, E., Rockwell, V.A., 2002. Value estimates of commercial mushrooms and timber in the Pacific Northwest. Env. Manage. 30:129-141.

Barros, L., Baptista, P., Ferreira, I.C.F.R., 2006. Influence of the culture medium and pH on the growth of saprobic and ectomycorrhizal mushroom mycelia. Minerva Biotec 18:165-70.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. Lme4: Linear mixed effect models using Eigen and S4. R package version1.1-6. http://CRAN.R-project.org/package=lme4

Boa, E., 2004. Wild Edible Fungi: A global overview of their uses and importance. FAO, Rome. http://www.fao.org/docrep/007/y5489e/y5489e00.htm

Bonet, J.A., de-Miguel, S., Martínez de Aragón, J., Pukkala, T., Palahí, M., 2012. Immediate effect of thinning on yield of *Lactarius* group *deliciosus* in *Pinus pinaster* forests in Northeastern Spain. For. Ecol. Manage. 265:211-217.

Bonet, J.A., Fischer, C.R., Colinas, C., 2004. The relationship between forest age and aspect on the production of sporocarps of ectomycorrhizal fungi in *Pinus sylvestris* forests of the Central Pyrenees. For. Ecol. Manag. 203:157-175.

Bonet, J.A., Palahí, M., Colinas, C., Pukkala, T., Fischer, C.R., Miina, J., Martínez de Aragón, J., 2010. Modeling the production and species richness of wild mushrooms in pine forests of the Central Pyrenees in Northeastern Spain. Can. J. For. Res. 40:347-356.

Bonet, J.A., Pukkala, T., Fischer, C.R., Palahí, M., Martínez de Aragón, J., and Colinas, C., 2008. Empirical models for predicting the production of wild mushrooms in Scots pine (*Pinus sylvestris* L.) forests in the Central Pyrenees. Ann. For. Sci. 65:206.

Bravo, F., Álvarez-González, J.G., Del Rio, M., Barrio-Anta, M., Bonet, J.A., Bravo-Oviedo, A., Calama, R., Castedo-Dorado, F., Crecente-Campo, F., Condés, S., Diéguez-Aranda, U., González-Martínez, S.C., Lizarralde, I., Nanos, N., Madrigal, A., Martinez-Millán, F.J., Montero, G., Ordóñez, C., Palahí, M., Piqué, M., Rodriguez, F., Rodriguez-Soalleiro, R., Rojo, A., Ruiz-Peinado, R., Sánchez-González, M., Trasobares, A., Vázquez- Piqué, J., 2011. Growth and yield models in Spain: Historical overview, contemporary examples and perspectives. For. Sys. 20:315-328.

Cai, M., Pettenella, D., Vidale, E., 2011. Income generation from wild mushrooms in marginal rural areas. For. Policy Econ. 13:211-226.

de-Miguel, S., Bonet, J.A., Pukkala, T., Martínez de Aragón, J., 2014. Impact of forest management intensity on landscape-level mushroom productivity: A regional model-based scenario analysis. For. Ecol. Manage. 330:218-227.

Espigol, R., 1999. Estado actual del cultivo de *Lactarius deliciosus*. In: Cultivo de hongos comestibles micorrícicos (Colinas, C., and Fischer, C. eds). Universidad de Lleida. Pp. 125-130.

Fang, Y., 2011. Asymptotic equivalence between cross-validations and Akaike Information Criteria in mixed-effects models. Journal of Data Science 9:15-21.

Fernández-Toirán, L.M., Ágreda, T., Olano, J.M., 2006. Stand age and sampling year effects on the fungal fruit body community in *Pinus pinaster* forests in Central Spain. Can. J. Bot. 84:1249-1258.

González-Ochoa, A.I., de las Heras, J., Torres, P., Sánchez-Gómez, E., 2003. Mycorrhization of *Pinus halepensis* Mill. and *Pinus pinaster* Aiton seedlings in two commercial nurseries. Ann. For. Sci. 60:43-48.

Hamilton, D.A., Brickell, J.E., 1983. Modeling methods for a two-state system with continuous responses. Canadian Journal of Forest Research 13:1117–1121.

Hernández-Rodríguez, M., de-Miguel, S., Pukkala, T., Oria-de-Rueda, J.A., Martín-Pinto, P. 2015. Climate-sensitive models for mushroom yields and diversity in *Cistus ladanifer* scrublands. Agricultural and Forest Meteorology 213:173-182.

Martínez de Aragón, J., Bonet, J.A., Fischer, C.R., Colinas, C., 2007. Productivity of ectomycorrhizal and selected edible saprotrophic fungi in pine forests of the pre-Pyrenees Mountains, Spain: predictive equations for forest management of mycological resources. For. Ecol. Manage. 252:239-256.

Martínez de Aragón, J., Riera, P., Giegiczny, M., Colinas, C., 2011. Value of wild mushroom picking as an environmental service. For. Policy Econ. 13:419-424.

Martínez-Peña, F., Ágreda, T., Águeda, B., Ortega-Martínez, P., Fernández-Toirán, L.M., 2012a. Edible sporocarp production by age class in a Scots pine stand in Northern Spain. Mycorrhiza 22:167-174.

Martínez-Peña, F., de-Miguel, S., Pukkala, T., Bonet, J.A., Ortega-Martínez, P., Aldea, J., Martínez de Aragón, J., 2012b. Yield models for ectomycorrhizal mushrooms in *Pinus sylvestris* forests with special focus on *Boletus edulis* and *Lactarius* group *deliciosus*. For. Ecol. Manage. 282:63-69.

Martínez-Peña, F., Gómez, C.R., Ortega-Martínez, P., 2007. MICODATA-Sistema de información geográfica sobre la producción, aprovechamiento y ordenación del recurso micológico en Castella y León. http://www.micodata.es

Mogas, J., Riera, P., Bennett, J., 2006. A comparison of contingent valuation and choice modeling with second-order interaction. J. For. Econ. 12:5-30.

Moore, G., Hall, D., Russell, J., 2001. Soil water. In 'Soilguide. A handbook for understanding and managing agricultural soils'. (ed. G. Moore), Agriculture Western Australia Bulletin No. 4343, pp. 80-93.

Ortega-Martínez, P., Martínez-Peña, F., 2008. A sampling method for estimating sporocarps production of wild edible mushrooms of social and economic interest. Investigación Agraria: Sistemas y Recursos Forestales. 17:228-237.

Palahí, M., Pukkala, T., Bonet, J.A., Colinas, C., Fischer, C.R., Martínez de Aragón, J., 2009. Effect of the inclusion of mushroom values on the optimum management of even-aged pine stands of Catalonia. For. Sci. 55:503-511.

Pilz, D., Molina, R., 2002. Commercial harvest of edible mushrooms from the forest of the Pacific Northwest United States: Issues, management, and monitoring for sustainability. For. Ecol. Manag. 155:3-16.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.URL http://www.R-project.org/.

Schulp, C.J.E., Thuiller, W., Verburg, P.H., 2014. Wild food in Europe: A synthesis of knowledge and data of terrestrial wild food as an ecosystem service. Ecol. Econ. 105:292–305.

Smith, J.E., Molina, R., Huso, M.M.P., Luoma, D.L., Mckay, D., Castellano, M.A., Lebel, T., Valachovic, I., 2002. Species richness, abundance and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age and old-growth stand of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, USA. Can. J. Bot. 80:186-204.

Snowdon, P., 1991. A ratio estimator for bias correction in logarithmic regressions. Can. J. For. Res. 21:720-724.

Straatsma, G., Ayer, F., Egli, S., 2001. Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. Mycol. Res. 105:515-523.

Voces, R., Diaz, B.L., Alfranca, O., 2011. Demand for wild edible mushrooms. The case of *Lactarius deliciosus* in Barcelona (Spain). J. For. Econ. 18:47-60.

Zamora-Martínez, M.C., Nieto de Pascual, C., 1995. Natural production of wild edible mushroom in southwestern rural territory of Mexico city, Mexico. For. Ecol. Manag. 72:13-20.

Figure captions

Figure 1. Study area. The red point denotes the "Pinares Llanos de Almazán" area, Soria province, Castilla y León region, in central Spain.

Figure 2. Inter-annual variability in edible mushroom yield. The horizontal line within each box indicates the median of edible mushroom yield for a particular year, whereas the bottom and upper lines of the box represent the 25th and 75th quantiles of annual mushroom yield distribution. The vertical dotted lines depict the data points that fall within the distance computed as quartile ±1.5*(interquartile range) from the extremes of the boxes.

Figure 3. Distribution of the accumulated rainfall from August to October over the occurrence of edible, marketed and *Lactarius* group *deliciosus* mushrooms, and distribution of pH over the occurrence of *Lactarius* group *deliciosus* sporocarps. The horizontal line within each box indicates the median, whereas the bottom and upper lines of the box represent the 25th and 75th quantiles of the distribution. The vertical dotted lines depict the data points that fall within the distance computed as quartile ±1.5*(interquartile range) from the extremes of the boxes.

Figure 4. Correlation matrix among the main variables (i.e., both response variables and predictors in their original scale) used in this study. Circle size denotes the correlation range from 0 to 1 or -1, whereas positive and negative correlations are shown using blue and red palettes, respectively. In the response variables, the term "yield" after Edible, Marketed and *Lactarius* denotes mushroom yield, whereas "pres" denotes a presence-absence of mushrooms. Regarding the meteorological variables, "P" denotes precipitation, "T" denotes mean temperature, "a", "s", "o" and "n" denote August, September, October and November, respectively. "OM" denotes organic matter content in the soil, whereas "Texture_1" and "Texture_2" denote loamy-sand and sandy-loam soil textures, respectively.

Figure 5. (A, C) Receiver operating characteristic (ROC) curve and area under the ROC curve (AUC) along with their bootstrapped 95% confidence intervals based on 2,000 bootstrap samples with replacement of the models for the probability of occurrence of edible and marketed mushrooms. (B, D) Ceteris paribus effects and associated uncertainty of precipitation on the probability of occurrence of edible and marketed mushrooms, respectively.

Figure 6. (A) Receiver operating characteristic (ROC) curve and area under the ROC curve (AUC) along with their bootstrapped 95% confidence intervals based on 2,000 bootstrap samples with replacement of the model for the probability of *Lactarius* group *deliciosus*. (B, C) Ceteris paribus effects and associated uncertainty of precipitation and soil pH on the probability of occurrence of *Lactarius* group *deliciosus*. (D) Combined effect of precipitation and pH on the probability of occurrence of *Lactarius* group *deliciosus* mushrooms.

Figure 7. Between-year variation in the probability of occurrence and yield conditional on the probability of occurrence of edible and *Lactarius* groups *deliciosus* sporocarps, as predicted by the year random effects of the models. *Lactarius* groups *deliciosus* figures show the between-year random variation on loamy sand soils of average acidity (i.e., mean pH in the data) on a stand of age equal to the mean stand age in the data.

Figure 8. Performance of the selected models for mushroom yield conditional on the probability of mushroom occurrence (Equations 3 and 4). The solid line represents perfect fit (1:1 equality line) whereas the dashed line indicates the regression line between the measurements and the back-transformed predictions of the selected model.

Figure 9. Ceteris paribus effects of meteorological and stand conditions on the yield of edible, marketed and *Lactarius* group *deliciosus* mushrooms as predicted by the hurdle models (i.e., product of Equations 1 and 3), and associated uncertainty. (A, B) Effect and associated uncertainty of the accumulated precipitation during late-summer and early-autumn on the yield of edible and marketed mushrooms. (C, D) Effect and associated uncertainty of stand age on marketed and *Lactarius* group *deliciosus* mushrooms.

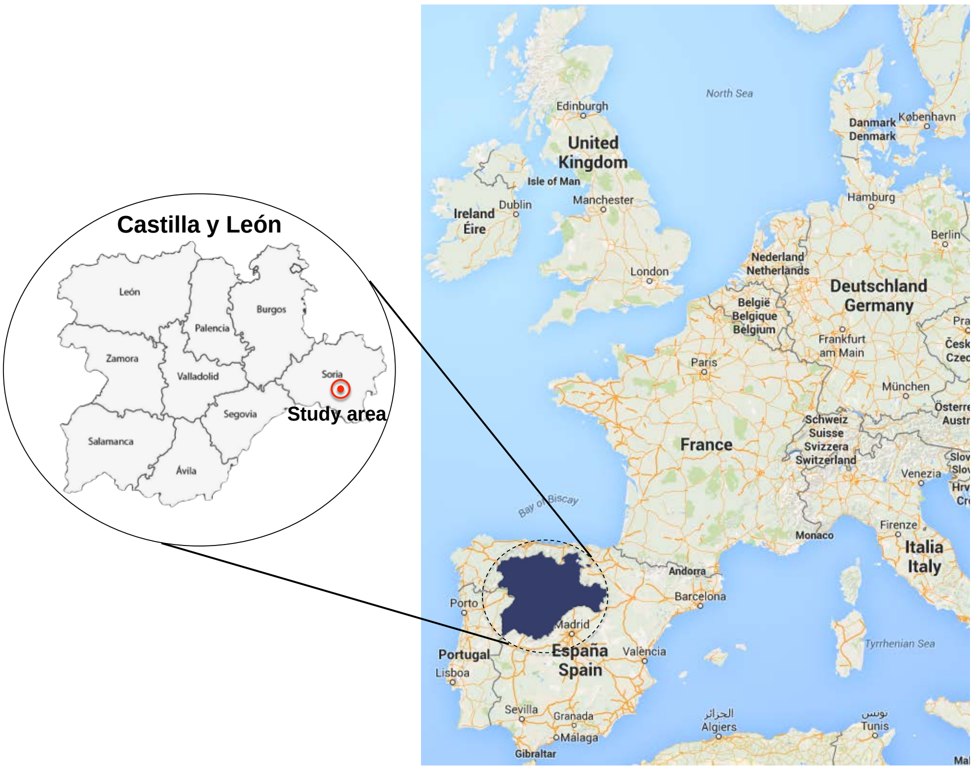
Castilla y León
León
Palencia
Burgos
Zamora
Valladolid
Soria
Segovia
Study area
Salamanca
Ávila
North Sea
Edinburgh
United Kingdom
Isle of Man
Manchester
Ireland
Éire
Dublin
London
Danmark
Denmark
København
Hamburg
Berlin
Nederland
Netherlands
België
Belgique
Belgium
Deutschland
Germany
Frankfurt am Main
Paris
München
France
Schweiz
Suisse
Svizzera
Switzerland
Venezia
Bay of Biscay
Monaco
Firenze
Italia
Italy
Andorra
Barcelona
Porto
Madrid
España
Spain
València
Portugal
Lisboa
Tyrrhenian Sea
Sevilla
Granada
Málaga
Gibraltar
الجزائر
Algiers
تونس
Tunis

Figure 1

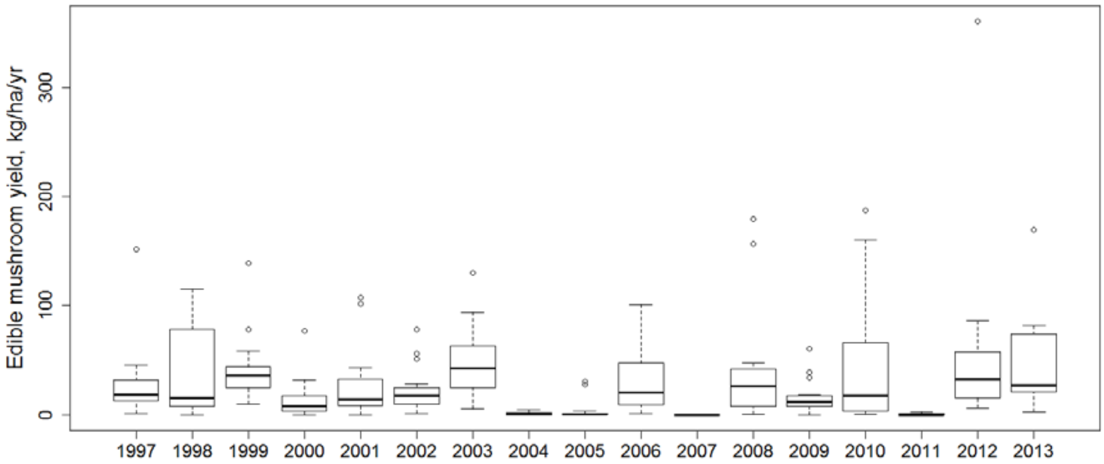
Edible mushroom yield, kg/ha/yr
0
100
200
300
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

Figure 2

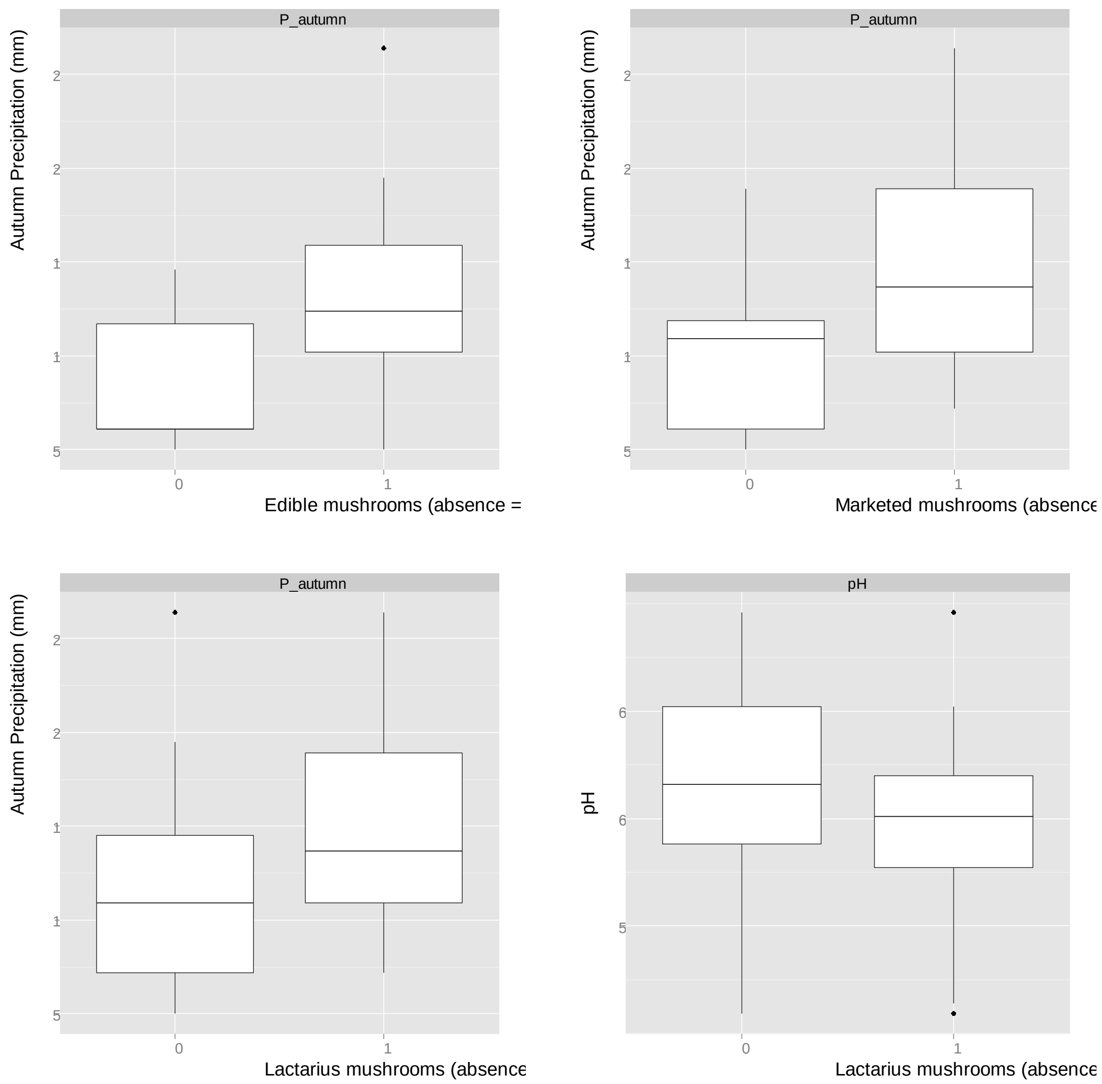
P_autumn
Autumn Precipitation (mm)
Edible mushrooms (absence =
P_autumn
Autumn Precipitation (mm)
Marketed mushrooms (absence
P_autumn
Autumn Precipitation (mm)
Lactarius mushrooms (absence
pH
pH
Lactarius mushrooms (absence

Figure 3

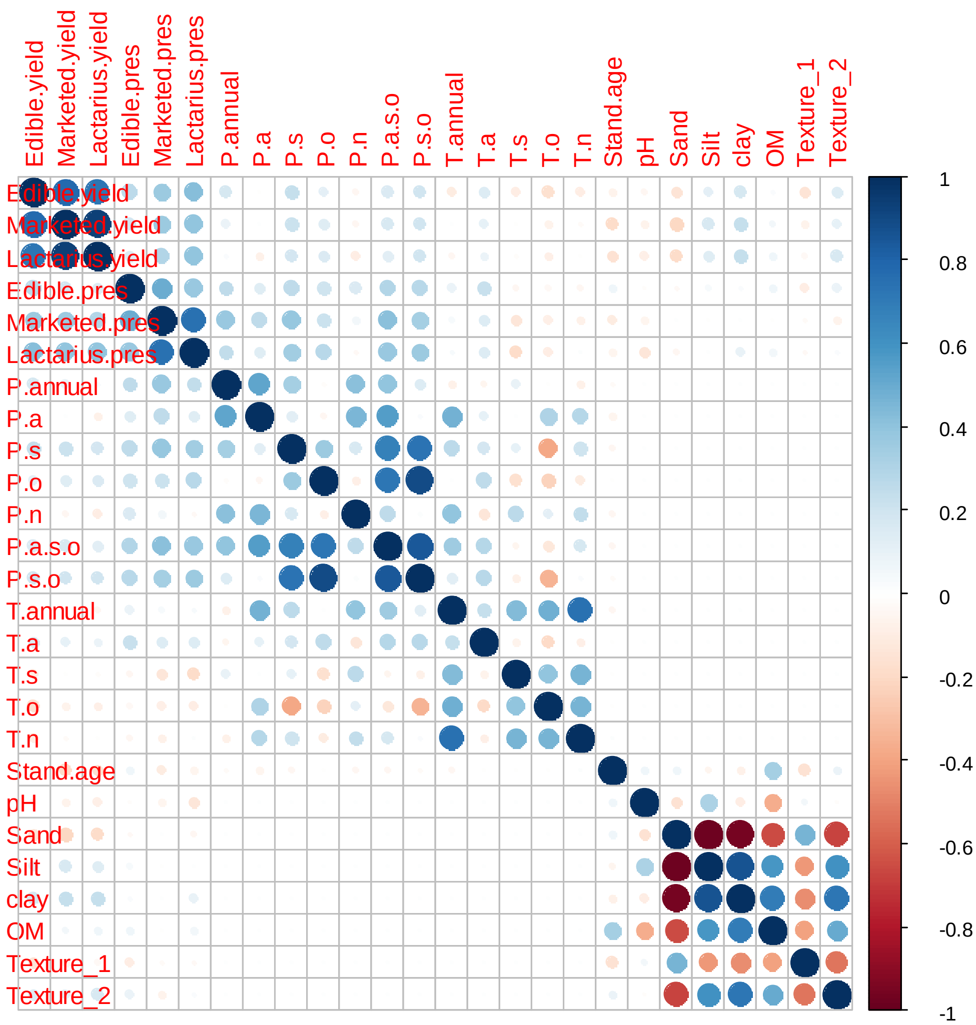
Edible.yield
Marketed.yield
Lactarius.yield
Edible.pres
Marketed.pres
Lactarius.pres
P.annual
P.a
P.s
P.o
P.n
P.a.s.o
P.s.o
T.annual
T.a
T.s
T.o
T.n
Stand.age
pH
Sand
Silt
clay
OM
Texture_1
Texture_2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

Figure 4

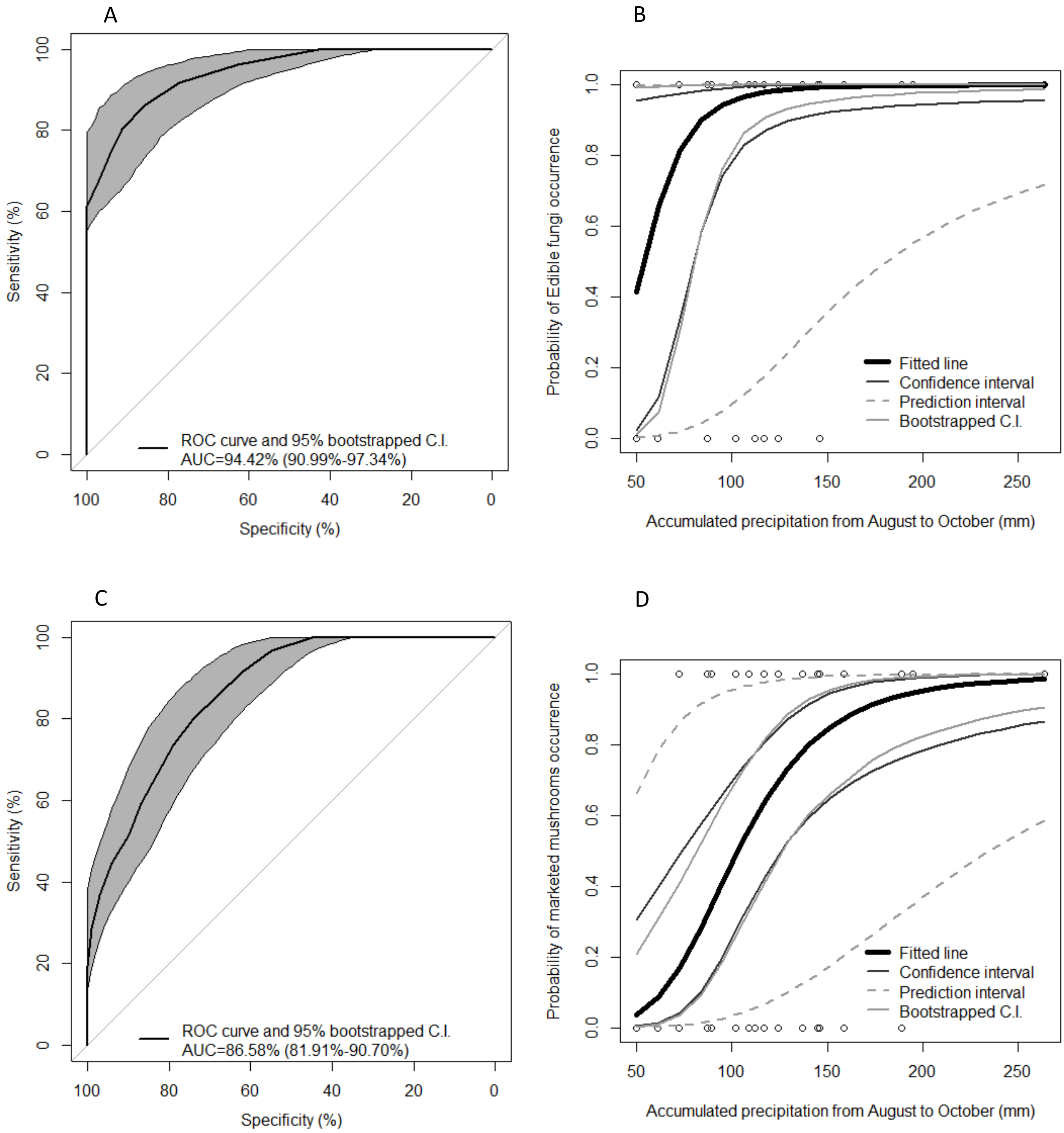
A
B
C
D
Sensitivity (%)
Specificity (%)
ROC curve and 95% bootstrapped C.I.
AUC=94.42% (90.99%-97.34%)
AUC=86.58% (81.91%-90.70%)
Probability of Edible fungi occurrence
Probability of marketed mushrooms occurrence
Accumulated precipitation from August to October (mm)
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.

Figure 5

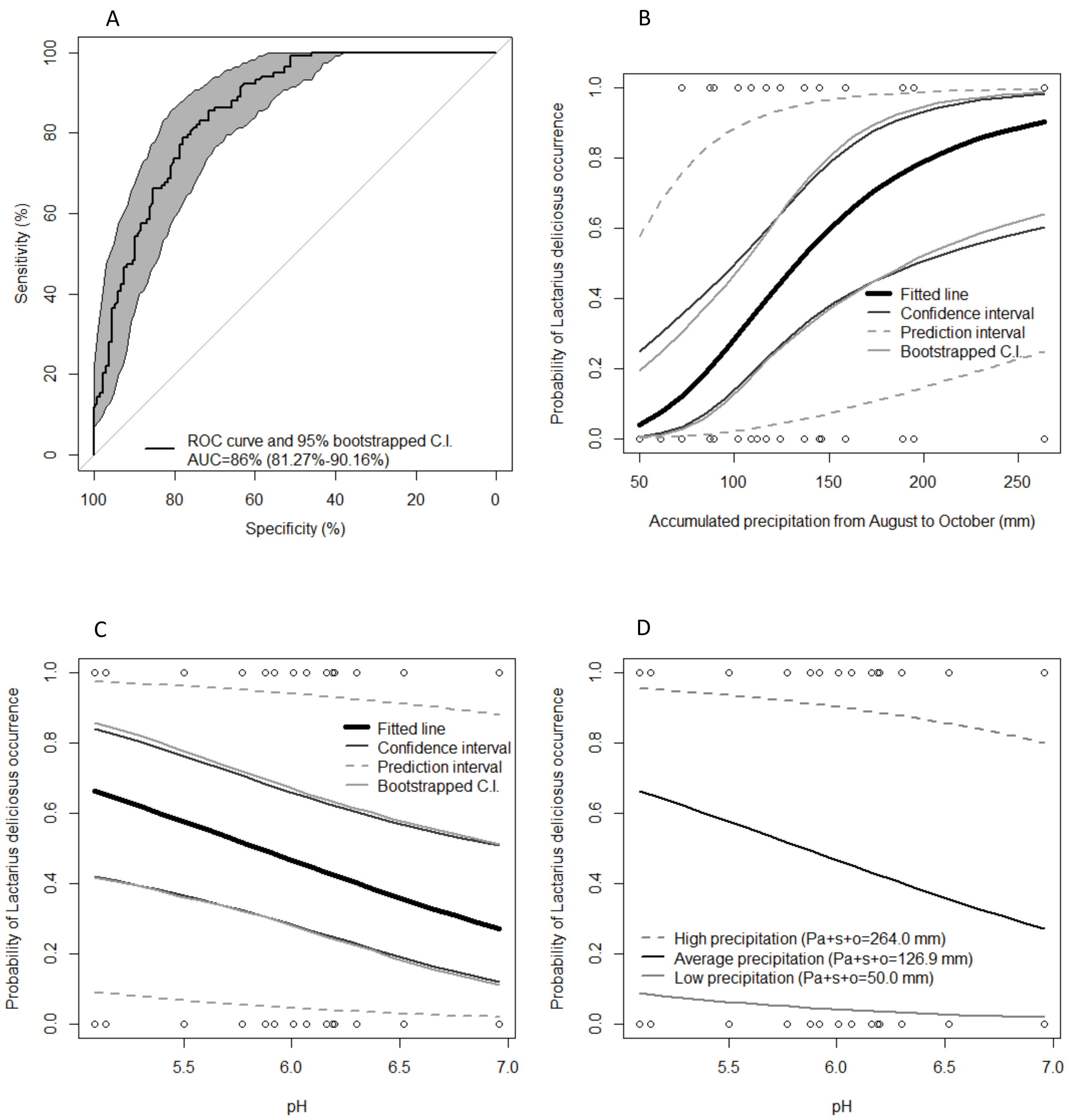
A
Sensitivity (%)
Specificity (%)
ROC curve and 95% bootstrapped C.I.
AUC=86% (81.27%-90.16%)
B
Probability of Lactarius deliciosus occurrence
Accumulated precipitation from August to October (mm)
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
C
Probability of Lactarius deliciosus occurrence
pH
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
D
Probability of Lactarius deliciosus occurrence
pH
High precipitation (Pa+s+o=264.0 mm)
Average precipitation (Pa+s+o=126.9 mm)
Low precipitation (Pa+s+o=50.0 mm)

Figure 6

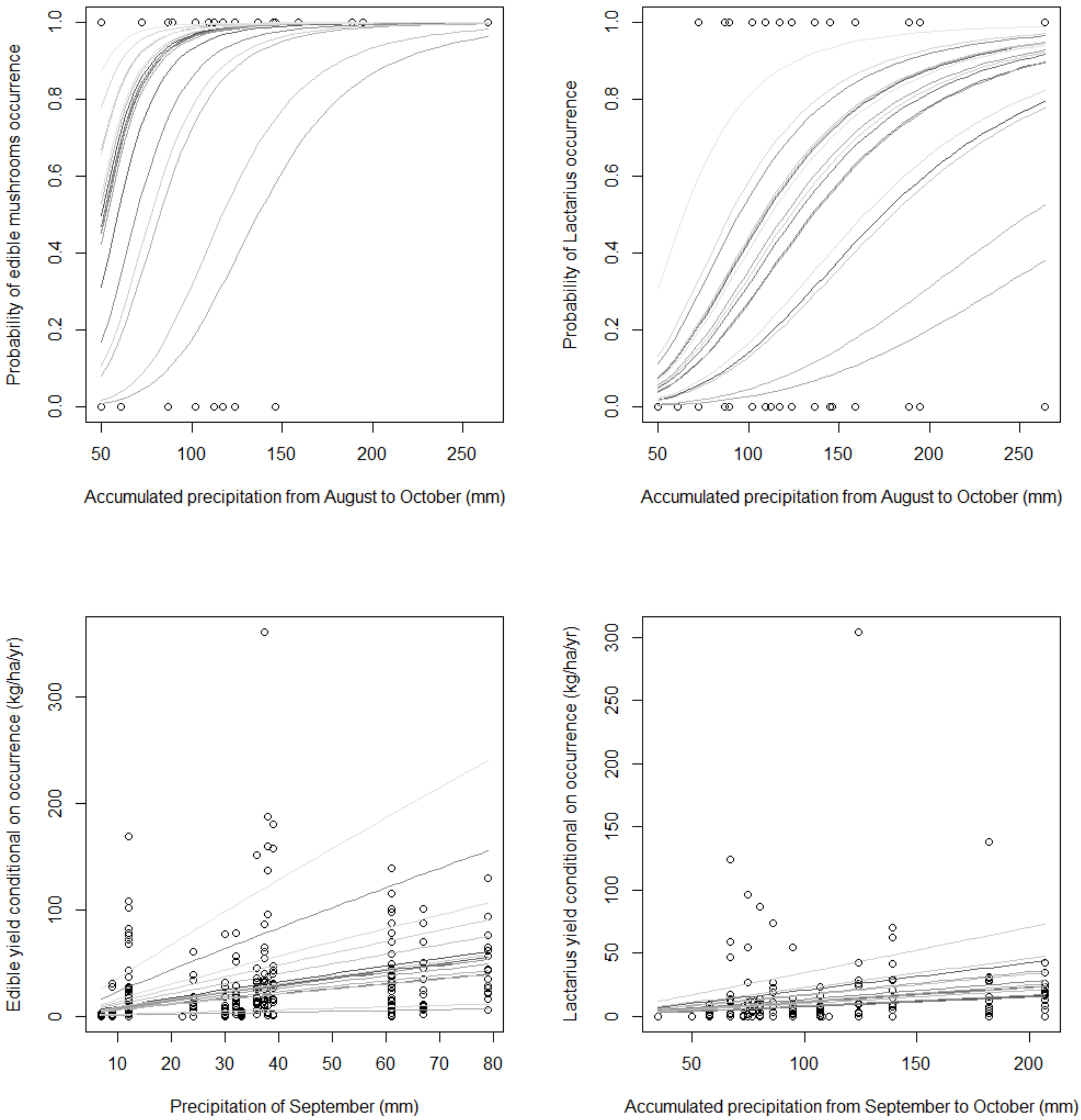
Probability of edible mushrooms occurrence
Accumulated precipitation from August to October (mm)
Probability of Lactarius occurrence
Accumulated precipitation from August to October (mm)
Edible yield conditional on occurrence (kg/ha/yr)
Precipitation of September (mm)
Lactarius yield conditional on occurrence (kg/ha/yr)
Accumulated precipitation from September to October (mm)

Figure 7

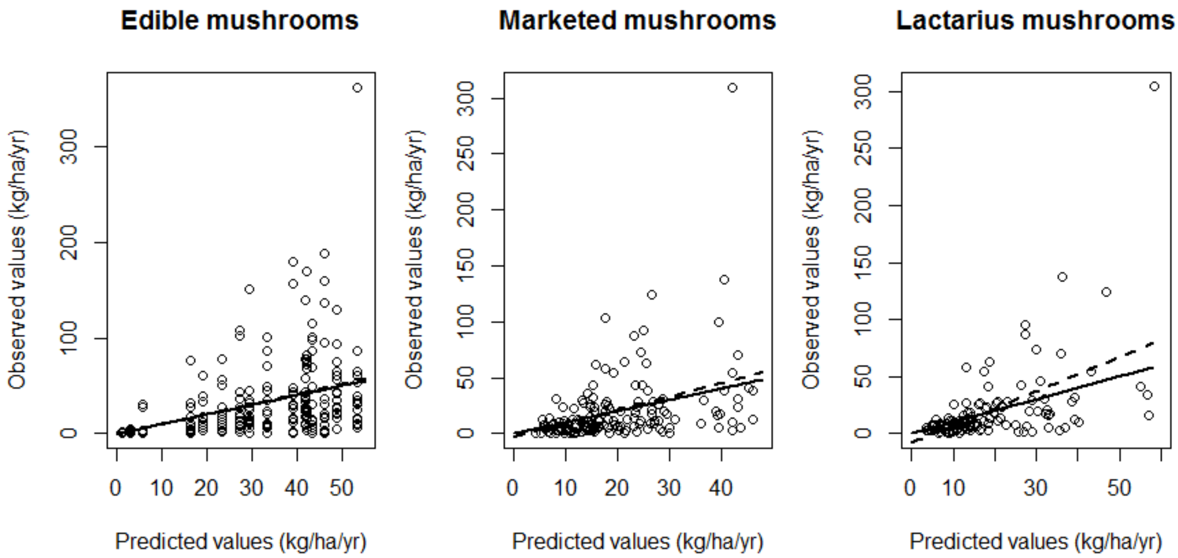
Edible mushrooms
Marketed mushrooms
Lactarius mushrooms
Observed values (kg/ha/yr)
Predicted values (kg/ha/yr)
0
100
200
300
0
50
100
150
200
250
300
0
10
20
30
40
50

Figure 8

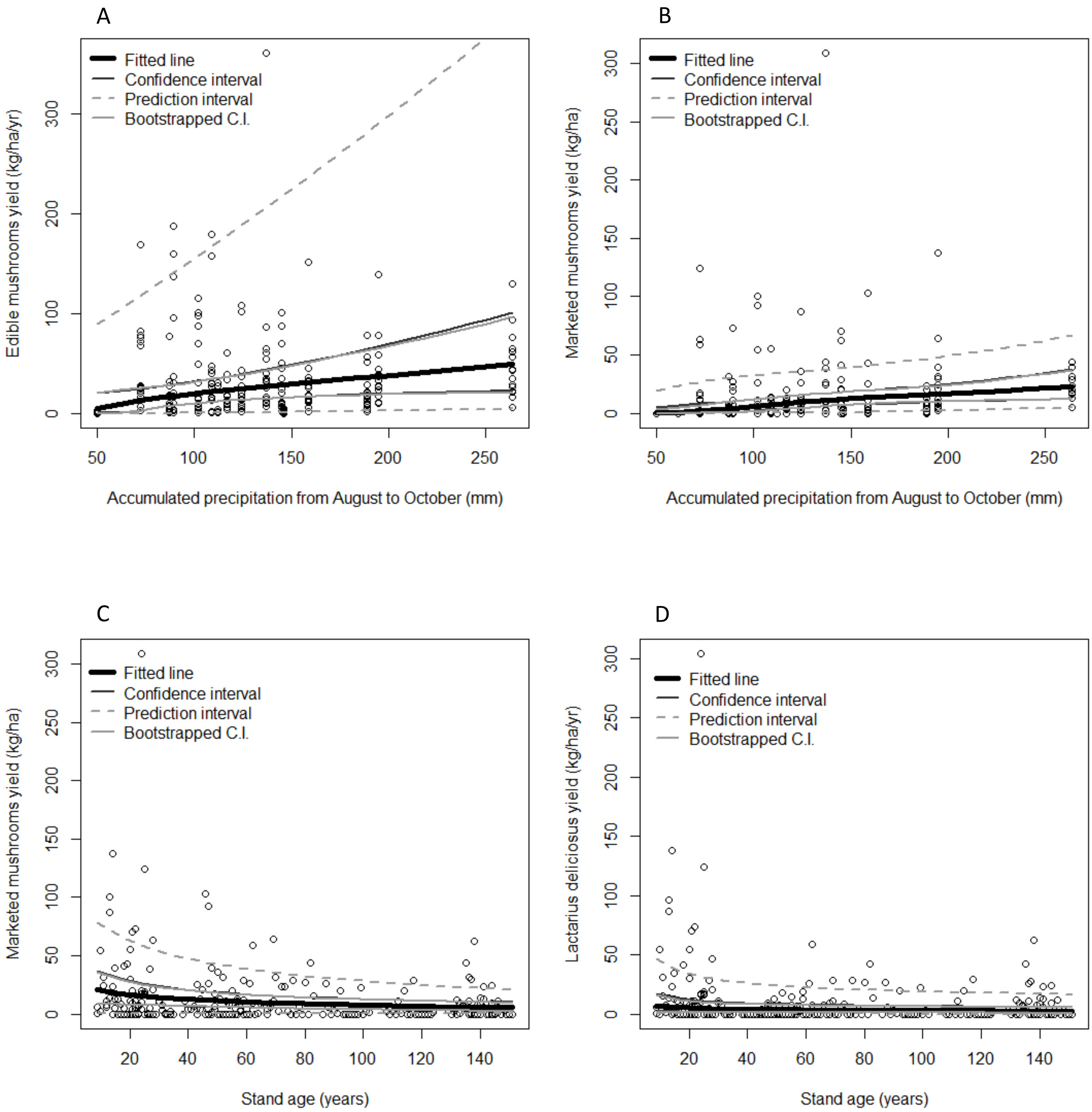
A
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
Edible mushrooms yield (kg/ha/yr)
Accumulated precipitation from August to October (mm)
B
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
Marketed mushrooms yield (kg/ha)
Accumulated precipitation from August to October (mm)
C
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
Marketed mushrooms yield (kg/ha)
Stand age (years)
D
Fitted line
Confidence interval
Prediction interval
Bootstrapped C.I.
Lactarius deliciosus yield (kg/ha/yr)
Stand age (years)

Figure 9

Table 1. List of the 41 edible and 8 marketed fungal species found in the study area (species with * are marketed species).

Edible and marketed fungal species identified in the study		
Agaricus impudicus	*Mycena galericulata*	*Russula xerampelina*
Agaricus sylvaticus	*Mycena pura*	*Suillus bellinii*
Amanita citrina	*Rhizopogon roseolus*	*Suillus granulatus*
Astraeus hygrometricus	*Rhodocollybia butyracea*	*Tricholoma fracticum*
Baeospora myosura	*Russula albonigra*	*Tricholoma ustale*
Chroogomphus rutilus	*Russula caerulea*	*Hygrophorus agathosmus**
Cortinarius delibutus	*Russula cessans*	*Lactarius deliciosus**
Hygrophoropsis aurantiaca	*Russula chloroides*	*Lactarius sanguifluus**
Hygrophorus gliocyclus	*Russula heterophylla*	*Lactarius semisanguifluus**
Laccaria laccata	*Russula risigallina*	*Macrolepiota procera**
Lactarius chrysorrheus	*Russula roseipes*	*Pleurotus eryngii**
Lycoperdon perlatum	*Russula turci*	*Suillus luteus**
Lyophyllum fumosum	*Russula vesca*	*Tricholoma terreum**
Macrolepiota konradii	*Russula violeipes*	

Table 2. Summary of the main data used in modeling.

Mushroom yield (kg ha^{-1} yr^{-1})	Mean	SD	Minimum	Maximum
Edible yield (kg ha^{-1} yr^{-1})	32.26	43.03	0.03	360.47
Marketed yield (kg ha^{-1} yr^{-1})	20.64	33.28	0.13	308.64
Lactarius yield (kg ha^{-1} yr^{-1})	20.64	35.11	0.59	303.95
Edible occurrence (prob.)	0.86	0.34	0.00	1.00
Marketed occurrence (prob.)	0.61	0.49	0.00	1.00
Lactarius occurrence (prob.)	0.46	0.50	0.00	1.00
August precipitation (mm)	28.45	27.77	3.00	101.00
September precipitation (mm)	35.26	20.60	7.00	79.00
October precipitation (mm)	63.22	31.96	14.00	128.00
pH	6.01	0.49	5.09	6.96
Stand age (years)	68.13	45.29	9.00	151.00
Sand (%)	88.57	5.23	76.84	93.84
Silt (%)	3.77	3.21	0.00	11.00
Clay (%)	7.65	2.21	6.16	13.16

Table 3. Fixed parameter estimates of the hurdle models describing the relationship between edible, marketed and *Lactarius* group *deliciosus* mushroom yield and meteorological, site and stand conditions in *Pinus pinaster* forests of central Spain. P_{s} is the precipitation of September, $P_{\mathrm{s+o\ o}}$ is the accumulated precipitation of September and October, $P_{\mathrm{a+s+o}}$ is the accumulated precipitation of August, September and October. All precipitation variables are in millimeters. *Age* is stand age (in years) represented by the age of the oldest tree in every plot. *pH* is soil pH, which represents the acidity (or alkalinity) of the soil. *LoamySand* and *SandyLoam* are two dummy variables (i.e., taking values 0 or 1) representing the corresponding loamy sand and sandy loam soil texture classes. The reference soil texture (i.e., when both dummy variables are zero) is sand. The terms “sqrt” and “ln” mean square root and natural logarithm, respectively. Parameter estimates are provided along with their standard errors and information on their p-values, as well as with the bootstrapped 95% confidence intervals based on 2,000 bootstrap samples with replacement. Statistical significance: *=P< 0.05; **=P< 0.01; ***=P < 0.001.

Model	Eq.	Predictor	Coeff.	Estimate	St. Error	Bootstrapped 95% conf. int.	
						Lower bound	Upper bound
Edible	1	Intercept	α_0	-19.602	10.321	-46.964	-1.713
		ln($P_{\mathrm{a+s+o}}$)	α_1	4.921*	2.249	1.318	11.143
	3	Intercept	β_0	-0.076	1.116	-2.277	1.798
		ln(P_{s})	β_1	0.925**	0.323	0.341	1.580
Marketed	1	Intercept	α_0	-20.923**	6.578	-37.525	-11.352
		ln($P_{\mathrm{a+s+o}}$)	α_1	4.514**	1.379	2.553	8.082
	3	Intercept	β_0	3.280***	0.386	2.442	3.975
		P_{s}	β_1	0.014*	0.007	0.001	0.029
		Sqrt(*Age*)	β_2	-0.142***	0.030	-0.197	-0.082
Lactarius deliciosus	1	Intercept	α_0	-10.543	5.457	-23.079	-1.553
		ln($P_{\mathrm{a+s+o}}$)	α_1	3.249**	1.085	1.500	6.075
		pH	α_2	-0.888**	0.337	-1.591	-0.209
	3	Intercept	β_0	-1.307	2.244	-5.920	2.977
		ln($P_{\mathrm{s+o}}$)	β_1	1.032*	0.479	0.137	2.000
		ln(*Age*)	β_2	-0.346***	0.101	-0.543	-0.146
		LoamySand	β_3	0.588**	0.206	0.185	1.002
		SandyLoam	β_4	0.960***	0.255	0.481	1.403

Table 4. Standard deviation of year random effects and residuals of the hurdle models describing the relationship between edible, marketed and *L.* group *deliciosus* mushroom yield and weather, site and stand conditions in *P. pinaster* forests. Estimates are provided along with the bootstrapped 95% confidence intervals based on 2,000 bootstrap samples with replacement.

Model	Equation	Parameter	Standard deviation	Bootstrapped 95% conf. int.	
				Lower bound	Upper bound
Edible	1	Year	2.560	0.885	6.606
	3	Residual	1.159	0.907	1.404
		Year	1.006	0.585	1.286
Marketed	1	Year	1.578	0.636	2.379
	3	Residual	1.159	0.854	1.470
		Year	0.482	0.238	0.832
Lactarius	1	Year	1.433	0.607	2.130
	3	Residual	0.955	0.7122	0.962
		Year	0.548	0.263	0.851